R EXD.

Vol. 88. Part 4. Pp. 119-138, 8 figs. 31st January, 1939.

IMP. INST. ENT.
— LIBRARY —
- 1 FEB 1939
SERIAL. En. 344
SEPARATE

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

PAGE

RAWAT, B. L., M.Sc., Ph.D. On the habits, metamorphosis and reproductive organs of *Naucoris cimicoides* L. (Hemiptera–Heteroptera) . . . . . 119–138, 8 figs.

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 4s. 6d.

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION 1938–1939.

J. C. F. Fryer, O.B.E., M.A., *President.*

H. M. Edelsten
A. D. Imms, M.A., Sc.D., F.R.S. } *Vice-Presidents.*
H. Willoughby Ellis, M.I.E.E.

Francis Hemming, C.M.G., C.B.E., *Treasurer.*

O. W. Richards, M.A., D.Sc., *Secretary.*

F. J. Griffin, A.L.A., *Registrar.*

Other Members of Council.

R. B. Benson, M.A.
Brig.-Gen. B. H. Cooke, C.M.G., C.B.E., D.S.O.
C. N. Hawkins.
L. G. Higgins, M.A., F.R.C.S.
B. M. Hobby, M.A., D.Phil.
Sir Guy A. K. Marshall, C.M.G., D.Sc., F.R.S.
N. D. Riley.
W. H. T. Tams.
W. R. Thompson, Ph.D., D.Sc., F.R.S.
B. P. Uvarov, D.Sc.
V. B. Wigglesworth, M.A., B.Ch., M.D.

Trustees of the Society.

R. W. Lloyd.
Sir Edward B. Poulton, F.R.S.

Finance and House Committee.

H. Willoughby Ellis, M.I.E.E. (Chairman).
Prof. P. A. Buxton, M.A.
Brig.-Gen. B. H. Cooke, C.M.G., C.B.E., D.S.O.
G. Fox-Wilson.
C. N. Hawkins.
R. W. Lloyd.

Publication Committee.

W. R. Thompson, Ph.D., D.Sc., F.R.S. (Chairman).
H. E. Andrewes.
M. Burr, D.Sc., F.G.S., A.R.S.M.
B. M. Hobby, M.A., D.Phil.
N. D. Riley.
V. B. Wigglesworth, M.A., B.Ch., M.D.

Library Committee.

R. B. Benson, M.A. (Chairman).
E. A. Cockayne, M.A., M.D., F.R.C.P.
H. M. Edelsten.
B. M. Hobby, M.A., D.Phil.
W. H. T. Tams.
B. P. Uvarov, D.Sc.

Committee for the Protection of British Insects.

W. G. Sheldon (Chairman).
Capt. E. Bagwell-Purefoy.
C. L. Collenette.
W. J. Dow.
J. C. F. Fryer, O.B.E., M.A.
Col. F. A. Labouchere.
N. D. Riley.
H. M. Edelsten (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

DELEGATES OF THE SOCIETY TO:

1. **British National Committee for Biology** (Royal Society).
   Sir Thomas Hudson Beare, LL.D., F.R.S.E., appointed 1933.
   Dr. Karl Jordan, F.R.S., appointed 1936.
2. **Conference of Delegates of Corresponding Societies of the British Association for the Advancement of Science.**
   Sir Edward Poulton, F.R.S., appointed 1937.
3. **International Congress of Entomology** (Berlin 1938).
   J. C. F. Fryer, O.B.E., M.A. *Francis Hemming, C.M.G., C.B.E.*
   A. D. Imms, M.A., Sc.D., F.R.S.
4. **Local Committee of Management of Wicken Fen.**
   Mr. H. M. Edelsten. *Mr. E. C. Bedwell.*
   [Delegates nominated by Committee for the Protection of British Insects.]
5. **National Trust for Places of Historic Interest or Natural Beauty.**
   Mr. W. G. Sheldon, appointed 1922.
6. **New Forest Association.**
   Mr. W. Fassnidge, appointed 1934.
7. **Royal Meteorological Society. Phenological Committee.**
   Dr. C. B. Williams, appointed 1937.

ON THE HABITS, METAMORPHOSIS AND REPRODUCTIVE ORGANS OF *NAUCORIS CIMICOIDES* L. (HEMIPTERA–HETEROPTERA)

By B. L. Rawat, M.Sc., Ph.D.

(Government of India Scholar.) Zoological Laboratory, Cambridge.

Communicated by Dr. A. D. Imms, F.R.S.

(Read 19th October, 1938.)

With Eight Figures.

Contents.

	PAGE
Introduction	119
Habits, etc.	120
Metamorphosis	123
The post-embryonic development of the genital efferent ducts and the genitalia	127
Reproductive system	133
Summary	137
Literature	138

Introduction.

Dufour described the general morphology of the reproductive organs of *Naucoris cimicoides*, and Schröder gave an account of these organs which is not in agreement with that of Dufour. A short note on the eggs and nymphs is given by Brocher (1913), and Rousseau (1921) has briefly described the nymphal instars. Apart from these accounts mention is made by Butler (1923) and a general account is given by Poisson (1924) but very little is known of the reproductive organs and the metamorphosis of this aquatic bug. In the present paper an account is given of its habits, reproductive organs and developmental instars. At the same time opportunity is taken of tracing the development of the genitalia and efferent ducts of the two sexes in *N. cimicoides*. In this connection it may be mentioned that while these parts have been studied to some extent in the Homoptera by Pruthi, George, and Metcalfe, the only study known to me in the Heteroptera is by Christophers and Cragg (1922) on the male genitalia of *Cimex*. An attempt has, therefore, been made in the following pages to study the development of the efferent ducts and genitalia in *Naucoris* in order to ascertain the facts regarding their nature and homology in the Heteroptera.

I am very grateful to Professor J. Stanley Gardiner for providing me with accommodation in the Zoological Laboratory, Cambridge. The work was undertaken at the suggestion of Dr. A. D. Imms, F.R.S., to whom I am indebted for his guidance and encouragement. I have also to thank Dr. W. H. Thorpe for suggestions and advice, and Dr. H. W. Lissman for his help.

As regards technique, aqueous Bouin's fluid and Carnoy's fluid proved successful as fixatives. Double-embedding gave poor results; softening of chitin by diaphanol and solvax also did not prove of advantage. For the study of the development of the genital ducts and the genitalia newly-moulted nymphs were fixed in picro-chlor-acetic acid. For staining orange G, iron haematoxylin,

Delafield's haematoxylin and eosin were used with good results. The nymphs were reared in small petri-dishes, in water which was changed every day.

Habits, etc.

Naucoris cimicoides is a dorsally flattened aquatic bug almost oval in outline and about 15 mm. long. The female is slightly larger than the male. It is found in fresh-water ponds and ditches, where it occurs in the vegetation near the banks. Poisson, as well as Morley, records it from brackish water also. Its dark brown colour on the dorsal surface renders it inconspicuous among the dead and decaying vegetation, and for the same reason it often escapes detection in the net. It generally lives under the surface of the water, clinging to vegetation, frequently coming to the surface for breathing. It can also be seen floating on the surface with its hind legs spread out in characteristic fashion. It is a powerful swimmer, swimming with the help of its posterior two pairs of legs, the anterior pair being modified for seizing and holding its prey. On land it walks quite rapidly, though clumsily, with its three pairs of legs in the style typical of an insect.

Rousseau mentions that *N. cimicoides* flies at night. Though I kept insects in the aquarium and observed them during the day as well as the night, none was seen taking to its wings, and indeed, with the absence of muscles of flight, I cannot understand how the insect can fly. Poisson also came to a similar conclusion. Kramer did not observe flight himself, but suggested that they do fly, since he found bugs migrating from one pond to another. It is very probable that they migrated by crawling on dry land from one pond to the other, as they have been found to do from one room to another in the laboratory. He omitted to mention the species he worked on, but from his references, it appears that he also dealt with *N. cimicoides*.

It is a predacious insect and preys on animals as tiny as *Daphnia* and *Cyclops* as well as animals of its own size and slightly bigger ones like *Nepa*. Kramer reported that it feeds on snails and fishes in addition. In the laboratory it was fed on the crustaceans *Gammarus* and *Asellus*, on which it thrived. In the absence of other food, it even turns cannibal, and feeds on dead insects of its own kind as well as others. It was also fed on pieces of meat, but never took to a vegetarian diet. The prey is held in the anterior pair of legs, and, if living, is paralysed and killed apparently by poison introduced into a puncture made by the stylets. It can remain without food for days, and during spring-time even copulation and egg-laying may continue normally without the insect taking any food.

When handling the insect one needs to be careful, since it may inflict a sharp and painful puncture, causing a sensation very similar to that caused by a scorpion sting, but, unlike the latter, the effect passes off after a short time.

Although this bug is easily obtainable at almost any time of the year, it is less easy to secure specimens during the months of winter. The reason for this is that it buries itself in the mud on the bank or creeps under vegetation. On a sunny but very cold wintry day, it has been possible to fish out a few *Naucoris* by breaking the layer of ice formed on the surface of the pond.

Copulation. Copulation begins late in February, though not so frequently as during the following months of spring and early summer. There is no courtship preliminary to copulation, and the male seizes the female as soon as it is near. On several occasions it was observed that a male got hold of another

male and rode on its back, as it does on a female, for copulation, but immediately dismounted. It is, however, not known by what indicators the female is recognised by the male.

The male alone appears to take an active part in copulation. It catches suddenly the female with its front pair of legs in the region of the mesothorax and sits on its back. Sometimes, in attempting to do so, the male may get dislodged by the actively swimming female, but once the male gets a correct hold, the female appears unmindful of its load. Although usually quiet, it sometimes swims, carrying the male on its back, or even catching prey and feeding. The male does not take part in swimming.

After it has gained its hold, the male projects its last segments posteriorly and always to the left of the female. Kramer mentioned that the organ is bent to the right of the female. His account, however, as mentioned before, does not mention the species to which he is referring. In *N. cimicoides* copulation was observed many times during the summers of 1937 and 1938, and in all cases the male always directed the abdomen to the left of the female. After bending its segments, the male bends them down below the hind segments of the female in such a fashion that the ninth segment, which protrudes behind the last segment, is applied against the ovipositor of the female. The aedeagus, which is brought out in this act, enters the space between the seventh sternum and the ovipositor, and its anterior or beak-like end enters the female aperture. The parameres are slightly raised and their distal ends are applied against the first valvula of the ovipositor. The conjunctiva lies everted in the vagina with its papillae and spiny plates serving to strengthen its hold therein. The distal end of the ductus ejaculatorius—the vesica—comes to lie dorsally into the bulbous part of the receptaculum seminis. The act goes on intermittently for 3–4 hours, the male remaining seated on the back of the female during the period. The copulating pair, unless shaken violently, is not disturbed, and can be easily fixed in this act by suddenly throwing them into boiling water. Copulation may take place at any hour.

Oviposition. Although copulation starts as early as February, oviposition does not begin until the middle of April. In the act of oviposition the female sits on the stem of an aquatic plant such as *Ranunculus* sp. or water peppermint. It holds the stem with its fore and middle pairs of legs—the hind pair simply resting on the stem. Sitting in this position, the insect lowers the tip of its abdomen against the surface of the stem and moves it slightly forward and then backwards, inserting the egg in the stem. The female then moves forwards and repeats the process. According to Poisson, the eggs are directly attached to a submerged object, while Butler and Kramer state that they are attached to the leaves of aquatic plants. In spite of careful observations, these accounts could not be confirmed.

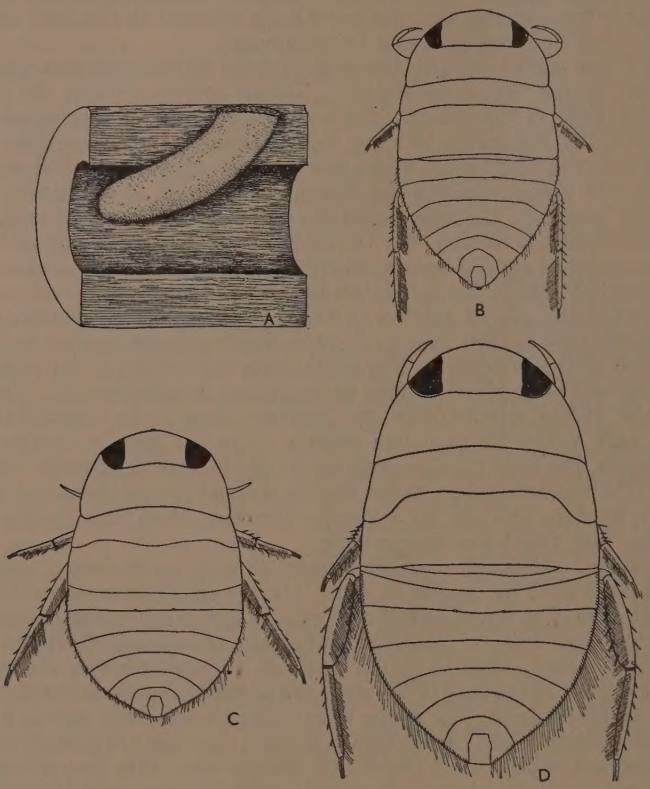
The egg is about 2 mm. long and is cylindrical in form, with a recurved end, which is covered with a lid having characteristic markings (fig. 1, A). The egg, as inserted, lies almost flush with the surface of the stem (fig. 1, A); Brocher and Régimbart mention that one-quarter of the egg protrudes outside the stem.

Oviposition continues until the beginning of July, and young nymphs are found up to about the middle of September. The majority of nymphs attain maturity about the end of September and by October hardly any nymphs are to be found.

Eclosion and moulting. The entire development from the time of the laying of the egg to the last ecdysis takes about 95 days, of which 30–34 days are passed in the egg.

The eyes of the developing embryo can be seen early through the egg shell. They are seen moving from side to side in the egg some time before eclosion. The outline of the developing embryo with its legs, rostrum, etc., are also visible through the egg shell towards the end of its developmental period.

The first sign of eclosion is the slight separation of the lid from the egg. The lid is ultimately forced apart by the head of the emerging nymph, which is covered by a membrane. This membrane continues to expand like a soap



1

FIG. 1.—A, longitudinal section of a stem of *Ranunculus* with the egg *in situ*. B, C and D, dorsal views of the first, second and third nymphal instars respectively.

bubble until there is a space between the head and the membrane. During this time the region of the head between the eyes begins to pulsate, and the head gradually emerges, ultimately fitting in this membranous vesicle. Almost as soon as the head fits in the vesicle, the membrane bursts and the nymph emerges more rapidly. The cephalic pulsations continue and the nymph emerges by moving itself vigorously backwards and forwards. When it has drawn itself out of the egg shell, it withdraws itself from the membrane which covers its body. Having withdrawn from the membrane, it sits on an adjoining

stem. The whole procedure takes about 20–25 minutes. As it comes out, it is very pale yellow in colour, but assumes its characteristic pigmentation within two hours.

The nymph undergoes five ecdyses before becoming an imago. Some time before each moult the nymph stops feeding and becomes sluggish. While moulting it floats with its ventral surface uppermost and with all its legs spread out. During this process the nymph arches its back, thereby splitting the old cuticle in the region of the mesothorax. The split spreads anteriorly to the head and posteriorly to the metatergum. It pushes out its thorax and head and also gradually pulls forwards its abdomen and legs until it completely emerges from its old exuviae. The newly-ecdysed nymph is pale yellow in colour and its alimentary canal is full of air bubbles: probably it sucks in air to help in moulting. Moulting takes about half an hour.

The following table gives the time taken by each nymphal instar. This was measured during the months of May to August at ordinary room temperature, which varied between 14° and 23° C.

Stadium	I	II	III	IV	V
Duration in days . .	12–13	6–8	7–9	14–16	21–23

Metamorphosis.

First nymphal instar (fig. 1, B).

The first stage nymph on emergence is about 3 mm. long and pale yellow in colour. It is similar to the imago in its general habits and feeds on small animals such as *Daphnia*, *Cyclops*, etc. In the laboratory it was fed on *Chironomus* larvae (the older instars, viz. 4 and 5, were fed on *Asellus*). The structure of the head is similar to that of the adult. Internally the pump is not fused with the dorsal wall of the head. The posterior arm of the endoskeleton is not fused with the margin of the occipital foramen as it is in the adult. The mesothorax forms the smallest and the metathorax the largest of the thoracic segments. The protergum is similar to that of the imago, but only laterally overlaps the mesosternum. The sternum is also similar to that of the imago. In the intersegmental membrane between the prothorax and mesothorax lies the first spiracle.

The tergum of the mesothorax is undivided. Its postero-lateral margins, which indicate the elytra rudiments, slightly project over the metatergum. The sternum is similar to that of the adult; it is fused laterally with the episternum. The epimeron is a simple plate and carries the second spiracle, but, unlike the adult, it does not develop a dorsal process. The metatergum is the largest of the thoracic tergal plates, and overlaps the first two abdominal segments posteriorly. It does not show any division into sclerites nor any indication of the wing rudiments. The sternum is similar to that of the adult. The episternum, which is fused with the sternum, is separated from the epimeron by a suture. The epimeron, unlike that in the adult, is visible ventrally and does not extend dorsally. This plate is partially covered from the ventral side by the projecting second abdominal tergum.

The prothoracic legs are similar to those of the imago. The femoral groove, in which the tibio-tarsal segment lies, is lined on either side by short peg-like spines intermixed with fine hair. The thick hairy area on the posterior

face of the femur is not developed. The second and third pairs of legs have only one tarsal segment and, moreover, only the dorsal surface of the tibia and the tarsus bear the linear series of long natatory hair.

The abdomen consists of eleven well-developed segments. The tergum of the first segment is not fused with that of the second segment, but forms a separate plate. Except for this difference, the structure of the first nine segments is similar to that of the adult. Tiny apertures of the repugnatorial gland appear on either side of the middle line between the third and fourth tergites.

The tenth tergum forms a small arched plate below the ninth, with which it is fused at its posterior margin. The tenth sternum is a narrow plate which is fused laterally with the tergum to form a ring, broad above and narrow below. The eleventh segment consists of a broad ventral plate and a poorly developed posteriorly pointed dorsal plate. Between the two lies the anus.

The male can be distinguished from the female by the presence of a small transverse ridge between the ninth and tenth sterna. This ridge is absent in the female (figs. 3, A and B).

The principal tracheal branches are as in the adult, but no air sacs are developed, nor is the parenchymatous tracheal organ yet developed. All the spiracles, except the second and third, are situated at the places they occupy in the adult. The second spiracle lies ventrally, being borne, as in the adult, by the epimeron. In the adult this is carried on the postero-lateral margin of the epimeron, behind the dorsal ridge. The third spiracle lies at the junction of the first and second sterna with the metathoracic epimeron.

The testes lead into the vasa deferentia, each of which ends in a swollen ampulla (*amp.*) on the ninth segment, there resting on the hypodermis. The hypodermal cells show a proliferation (fig. 4, A).

The ovaries on each side lead into the solid oviducts which end posteriorly in ampullae (*amp.*) in the seventh segment (fig. 4, B). The hypodermis on the eighth and ninth sterna forms a thick layer.

The succeeding nymphal instars resemble the first in the greater part of their anatomy except for the development of the reproductive efferent ducts, the genitalia, the wings and the parenchymatous tracheal organ. The development of the efferent genital ducts, the genitalia and the wings, is described in the following account.

Second nymphal instar (fig. 1, C).

The elytra rudiments appear on the postero-lateral edges of the mesotergum, but the wing rudiments have not yet appeared. The parenchymatous tracheal organ has not developed.

In the male there is formed an ectodermal invagination between the ninth and tenth sterna (fig. 3, B), the anterior blind end of this invagination consisting of hypodermal cells has extended anteriorly as far as the ampullae of the vasa deferentia (fig. 6, C).

In the female there is no change worth mentioning except that the hypodermal cells of the eighth and ninth segments have proliferated.

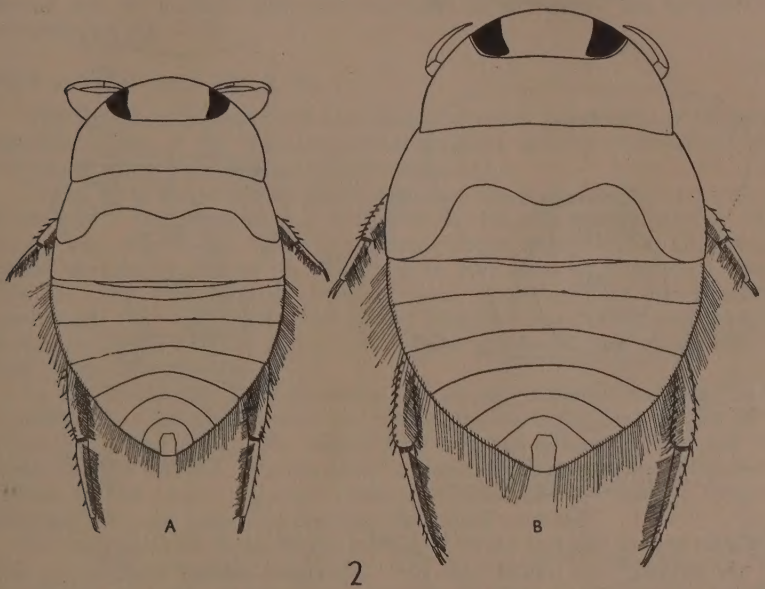
Third nymphal instar (fig. 1, D).

The elytral rudiments have increased and the wing rudiments have appeared on the postero-lateral margins of the metatergum. The parenchymatous

tracheal organ appears as tiny white bundles, one on either side of the mid line in the mesothorax.

In the male the ampullae at the ends of the vasa deferentia bud out on each side the future accessory gland (fig. 4, D).

The ectodermal invagination has extended anteriorly to lie between the terminal ampullae of the vasa deferentia (fig. 4, E); this is the future ejaculatory duct. The invagination between the ninth and tenth segments is bordered on either side by the greatly proliferated hypodermal cells which form the genital rudiment.



2

FIG. 2.—A. Dorsal view of the fourth and B of the fifth nymphal instars.

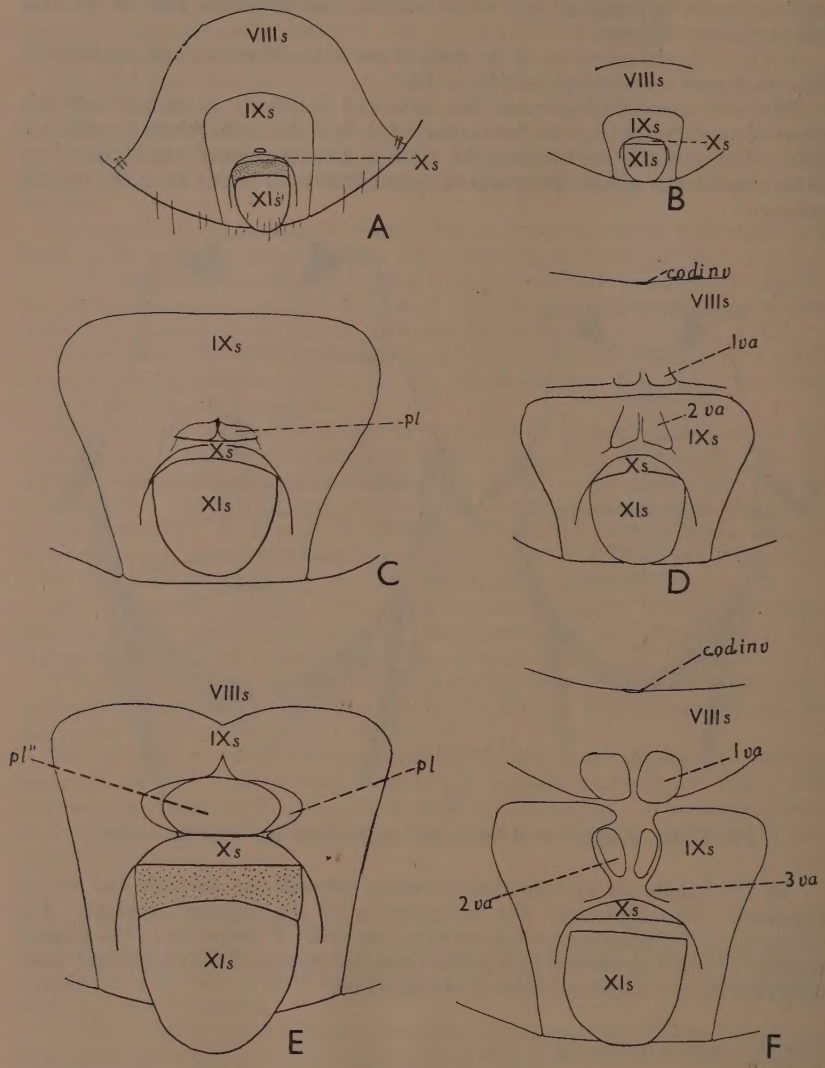
In the female an invagination develops between the seventh and eighth segments. This represents the invagination of the common oviduct. The blind end of the invagination lies between the oviducal ampullae in the seventh segment. The hypodermal cells at the posterior margin of the eighth and ninth segments form a thickened layer in the mid line.

Fourth nymphal instar (fig. 2, A).

The elytral rudiments have increased and posteriorly cover the rudiments of the wings.

The parenchymatous tracheal organ is quite prominent in the mesothorax.

The vasa deferentia lie on either side of the ejaculatory duct into which they ultimately open. The ejaculatory duct continues anteriorly beyond the place where the vasa deferentia opens into it; this is the future ectadenium. The accessory gland tubes also increase in length. The ejaculatory duct posteriorly communicates with the genital chamber. The penis lobes are clearly marked off and are distinguishable as such in a transverse section passing through the



3

FIG. 3.—A, C and E, ventral views of the last abdominal segments, in the male, of the first, fourth and fifth instars respectively: B, D and F, the same of the respective females.

c. od. inv., common oviducal invagination; *pl.*, penis lobe; *pl'.*, lobe which forms the parameres; *pl''.*, lobe which forms the aedeagus; *va.*, valvula—number denotes corresponding valvula; *s.*, sternum—number denotes the corresponding sternum.

region behind the ninth segment (fig. 6, A). In fig. 3, C, it will be seen clearly that the penis lobes lie in the intersegmental region between the ninth and tenth segments.

The invagination of the common oviduct lies between the oviducal ampullae which ultimately open into it (fig. 5, B). The rudiments of the ovipositor lobes of the eighth segment appear as two lobes, one on either side of the mid line. Each of these shows a further division into a median and lateral one (figs. 3, D and 5, D). The rudiments on the ninth segment also undergo similar divisions (figs. 3, D and 5, F). Behind the eighth segment between the bases of the medial pair of genital rudiments arises an invagination—the spermathecal invagination (fig. 5, E).

Fifth nymphal instar (fig. 2, B).

The elytral rudiments have increased and reach posteriorly as far as the anterior margin of the third abdominal segment thereby covering the wing rudiments which have also developed considerably.

In the male the accessory glands and the ectadenium have elongated and lie in coils. The penis lobe on each side divides into two—a median and a lateral lobe (fig. 3, E); these two lobes, though separated distally, remain united proximally (fig. 6, B). The median pair fuses to form the aedeagus (Pruthi). The tube, enclosed between them, forms the tube into which the ejaculatory duct continues. The lateral lobes develop further and form the parameres in the adult in which they remain in sclerotic connection with the base of the aedeagus (fig. 6, C).

In the female (fig. 3, F) the inner lobe of the ovipositor rudiment on the eighth segment develops further and ultimately forms the first valvula of the ovipositor in the adult. The lateral lobe does not develop further and only forms the first valvifer. On the ninth segment the inner lobe forms the second valvula of the adult ovipositor while the lateral one develops to form the third valvula; its basal part forming the second valvifer.

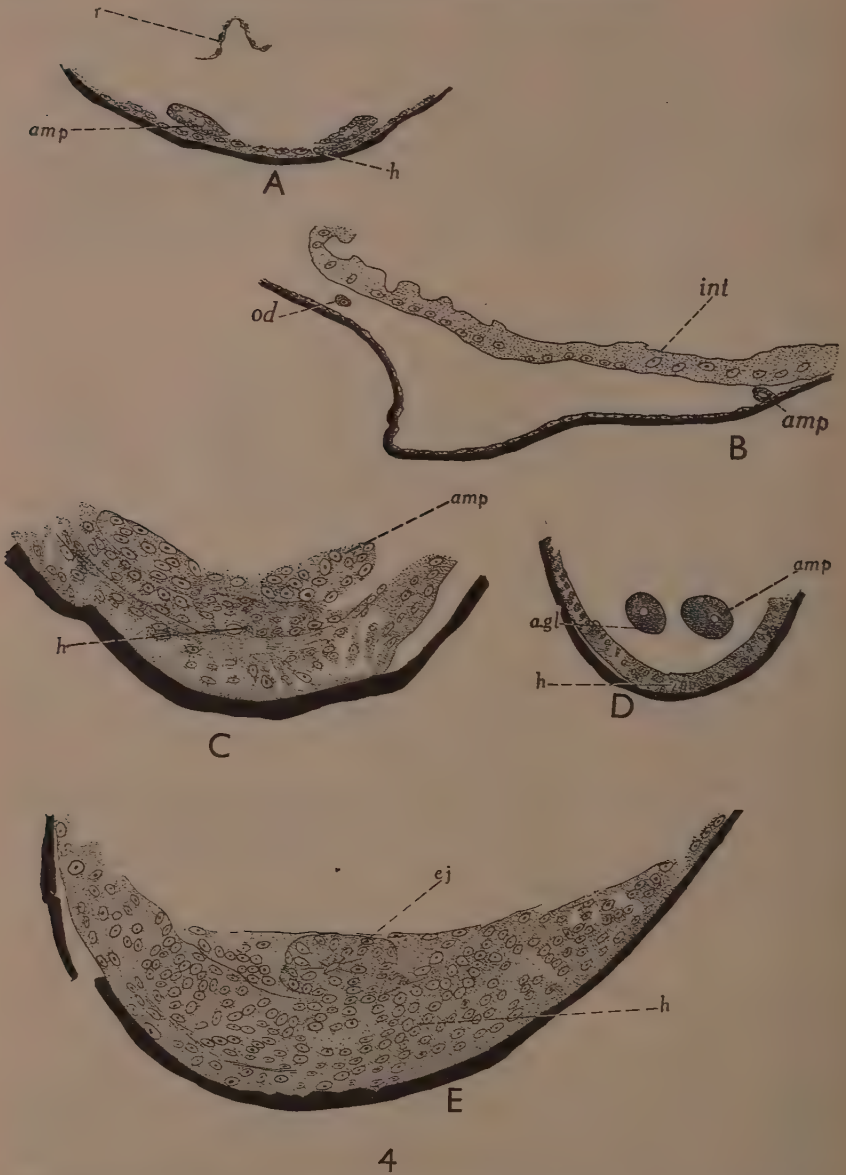
The spermathecal invagination lies dorsal to the common oviduct invagination and extends further anteriorly. The intervening wall between the two invaginations breaks down to form a common tube (fig. 6, D), thereby extending the common oviduct which opens behind the eighth segment. The distal part of the spermathecal invagination forms the spermatheca and no accessory gland is developed.

The Post-Embryonic Development of the Genital Efferent Ducts and the Genitalia.

The literature on the development of the efferent genital ducts and the genitalia in insects has been reviewed and discussed by Pruthi (1924), George (1928), Nel (1930), Metcalfe (1930–31), Else (1934) and Snodgrass (1931–37). In the following account only new contributions will be considered, reference being made to some of the more important findings of the earlier workers where necessary.

Female Genitalia.

As described previously, the genital rudiments arise as paired buds on the eighth and ninth abdominal segments. The pair on the ninth segment divides into two pairs as shown in figs. 3, D and 3, F. Similarly the pair on the eighth



4

FIG. 4.—Transverse sections through the abdomen. A, posterior region of ninth segment in first instar nymph, male. B, seventh segment in first instar nymph, female. C, posterior region of ninth segment in second instar nymph, male. D, posterior region of the abdomen in third instar nymph, male, showing the formation of the accessory glands. E, posterior region of the ninth segment in third instar nymph, male.
amp., ampulla—oviduct or vas deferens; *agl.*, accessory gland; *ej.*, ejaculatory duct; *h.*, hypodermis; *int.*, intestine; *od.*, oviduct; *r.*, rectum.

segment is differentiated into an outer and inner pair (fig. 3, D). In the subsequent course of development the inner pair on the eighth segment develops into the first pair of valvulae (anterior), while the outer one remains and forms only the first valvifer. The inner pair of buds on the ninth segment develops into the second pair of valvulae (posterior), while the outer one develops into the third pair of valvulae (lateral) and its base forms the second valvifer.

From this it will be clear that the first valvulae (or the gonapophyses of the eighth segment) are homologous with the second valvulae, while the third valvulae have no homologous counterpart on the eighth segment, since no valvula is developed thereon.

The first and second valvifers respectively represent the gonocoxites of the eighth and ninth segments of a Thysanuran, and the third valvulae represent the drawn-out processes of the gonocoxite of the ninth segment.

The work of Christophers and Cragg on *Cimex* and of George and Metcalfe on Homoptera is in agreement with the above conclusions arrived at for Heteroptera. Nel's conclusions in Orthoptera differ from these since he homologises the first valvulae (anterior) with the third valvulae (lateral). Denny's account, however, of *Blatta orientalis* is in complete agreement with my views.

Efferent ducts.

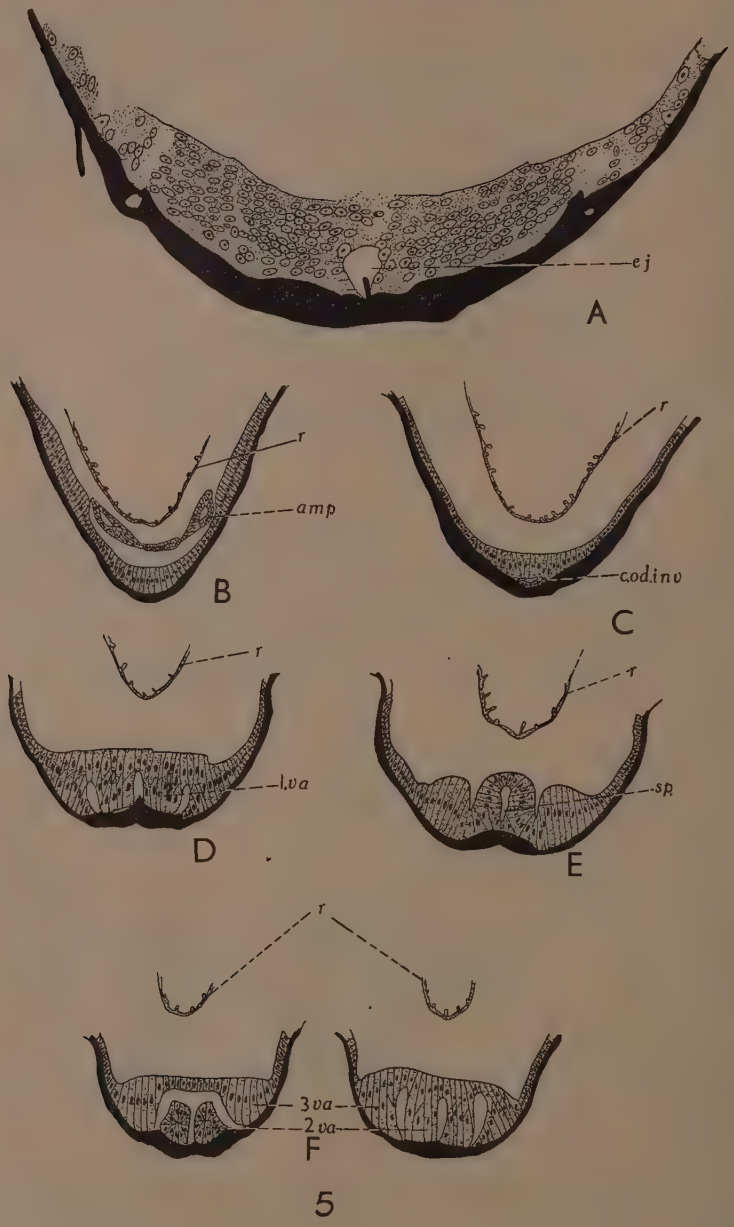
The lateral oviducts run from the ovaries up to the seventh abdominal segment, where they end in the mesodermic ampullae. Being derived from the primary genital strands, they are mesodermal in origin (Heymons, Wheeler, and others). As mentioned before, the common oviduct is formed by two parts; one part is formed by the common ectodermal oviducal invagination which arises between the seventh and eighth segments, and the other part is formed by the ectodermal spermathecal invagination arising between the bases of the first pair of valvulae. The two subsequently fuse to form the common median oviduct.

George's findings in respect to the mesodermal nature of the lateral oviducts in *Philaenus spumarius* L. are similar to those mentioned above. Later, Metcalfe, working on *Philaenus leucophthalmus* L. contradicted him by stating that the posterior part of the oviduct is ectodermal, since she regarded the mesodermic ampullae, as described by George, as a misrepresentation and called them the " anterior division of the unpaired oviduct."

In the first nymphal instar the lateral oviducts in *Naucoris* extend as far as the posterior margin of the seventh sternum, where they end in the mesodermic ampullae when the unpaired oviduct is not formed at all (fig. 4, B). This rules out any possibility of there being any " anterior division of the unpaired oviduct." Moreover, fig. 5, B, shows the ampullae lying on either side of the anterior blind end of the median oviducal invagination formed from behind the seventh sternum, into which they open ultimately.

Nel's conclusions as to the mesodermic nature of the entire lateral oviducts in Orthoptera are also in accordance with these facts. Metcalfe mentioned the replacement of the posterior part of the oviducts by ectodermal cells in *Dasyneura leguminicola* (Diptera). No such replacement was, however, observed in *Naucoris*.

The spermathecal invagination in *Naucoris* arises between the bases of the first pair of valvulae. Its proximal part forms the posterior portion of the common oviduct. Here again it is different from the spermatheca of *Philaenus spumarius* L. as described by George, who describes the spermatheca arising from the invagination behind the seventh segment, although Metcalfe described



5

a similar spermathecal development for *Philaenus leucophthalmus* from the invagination behind the eighth segment.

The definitive female genital pore lies in *Naucoris*, as in the other Homoptera, behind the eighth segment, though the primitive genital opening lies, as I believe for the majority of insects, between the seventh and eighth segments.

The above account serves to confirm the conclusions of Wheeler, George, Nel, and Metcalfe, that the ectodermal region of the efferent system is unpaired in origin and is not paired as described by Nüssbaum and later maintained by Pruthi.

Male Genitalia.

At the beginning on either side of the ectodermal invagination between the ninth and tenth segments there is developed a single pair of buds. These buds lie in the intersegmental region behind the ninth segment, and each is divided into an inner and outer bud, the two remaining united proximally. The inner one fuses with its fellow of the opposite side to form the aedeagus, while the outer one gives rise to the paramere. In Homoptera (Pruthi, George, and Metcalfe) there are developed—as appears from their figures—two appendicular processes in the same region. The outer of these two processes forms the sub-genital plate, while the inner one divides to form the aedeagus and the paramere. In *Naucoris* there is only one pair of buds which divide to form the aedeagus and the paramere. Therefore, this evidently represents the "penis lobe" (George) or "paramere lobe" (Pruthi) of Homoptera. The bud which gives rise to the sub-genital plate (limb base) in Homoptera is not developed at all.

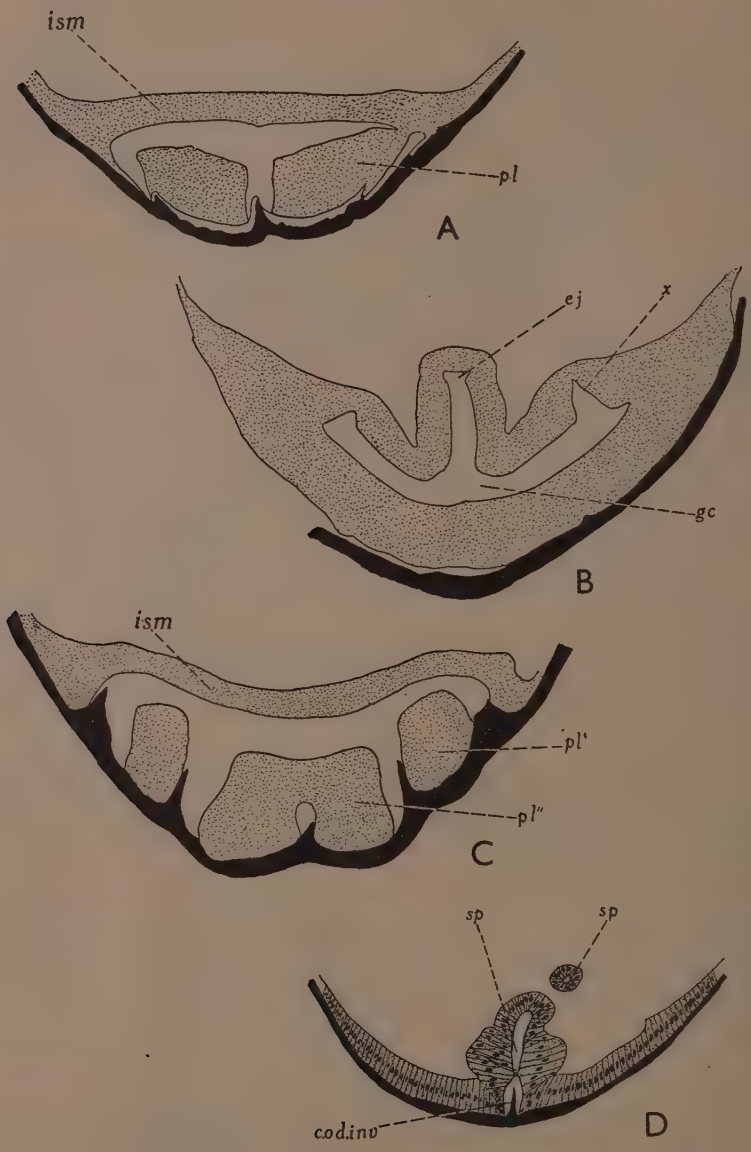
The male genitalia have been regarded as representing the gonapophyses of the ninth segment of a male Thysanuran or homologous with the second valvulae of the female ovipositor (George, Metcalfe, etc.). Recent embryological studies of Else (1934) on *Melanoplus differentialis* and Roonwal (1937) on *Locusta migratoria* have shown that the appendages of the tenth segment migrate anteriorly and medially and ultimately lie on the ninth segment to form the male genitalia.

It has been seen from the above account that the male genitalia in the post-embryonic development appear in the intersegmental region between the ninth and tenth segments. From their position and the available embryological evidence it is, therefore, reasonable to assume that they represent the appendages of the tenth abdominal segment.

Snodgrass (1935) termed the parameres, which in the adult are movable independently by muscles, harpagones, thereby calling them the homologues of the gonostyli of the ninth segment. The above account of their ontogenetic development, however, shows that this is not so. Moreover, his criterion that such processes, when independently supplied with muscles, are "harpes" or "harpagones," *i.e.* homologous with the Thysanuran abdominal styli of the ninth segment, does not hold good, at least in this suborder. From the above

Fig. 5.—Transverse sections through the abdomen. A, passing behind the region shown in E, fig. 4, in a third instar nymph, male. B, seventh segment in fourth instar nymph, female. C, posterior region of seventh segment in fourth instar nymph, female. D, posterior region of eighth segment in fourth instar nymph, female. E, passing behind the eighth segment in fourth instar nymph, female. F, posterior region of ninth segment in fourth nymphal instar, female—the left figure is that of a section taken posterior to that shown in the right figure.

amp., ampulla; *c. od. inv.*, common oviducal invagination; *ej.*, ejaculatory duct; *va.*, valvula—number denotes the corresponding valvula; *r.*, rectum; *sp.*, spermathecal invagination.



6

account it is also clear that the aedeagus is paired in origin. Accounts of Pruthi, George, and Metcalfe (Homoptera), Zander (Trichoptera and Hymenoptera), and Christophers and Cragg (Heteroptera) point to a similar development.

Efferent ducts.

There has been considerable controversy regarding the ectodermal and mesodermal nature of the efferent ducts, as well as the paired or unpaired origin of the ectodermal part of the efferent system.

Pruthi (Coleoptera and Homoptera), Metcalfe (Coleoptera and Homoptera), and Mehta (Lepidoptera) hold that the posterior part of the vas deferens (before it joins the ejaculatory duct) is ectodermal in origin, but, as is mentioned below, they differ about its formation.

In the first nymphal instar the primary efferent ducts extend up to the ninth segment, where they end in the mesodermic ampullae (fig. 4, A). They are, therefore, mesodermal in origin (Heymons, Wheeler). George found a similar condition in *Philaenus spumarius* L. (Homoptera) and doubted the presence of lateral ectodermal ejaculatory ducts as described by Pruthi in *Idiocerus*. Metcalfe regarded the ampullae, described by George, as the " primary divisions of the median ejaculatory duct." The two ampullae are shown in fig. 4, A; they form the posterior-most ends of the solid vasa deferentia resting on the hypodermis, which shows no development of the ejaculatory duct. There can, therefore, be no question of the ampullae being formed as divisions of the ejaculatory duct, since the latter is not formed at all at this stage. The existence of the paired lateral ectodermal ducts (Pruthi) must also be denied on the basis of this account of the post-embryonic development in *Naucoris*. George and Metcalfe also deny the presence of such separate ducts in Homoptera.

The accessory glands arise from the ampullae and are, therefore, mesodermal in origin and not ectodermal as Metcalfe mentions for *Philaenus leucophthalmus* or Pruthi for *Idiocerus*. George also disagrees with Pruthi and regards accessory glands as mesodermal in origin in *Philaenus spumarius*. Christophers and Cragg also call these glands mesodermal in *Cimex*.

A third unpaired gland is developed as an anterior continuation of the median ejaculatory duct. This is, consequently, ectodermal in origin. No such gland has so far been described for Hemiptera. In the male, as may be seen above, the ectodermal part of the efferent system is unpaired in origin and not paired as stated by Pruthi.

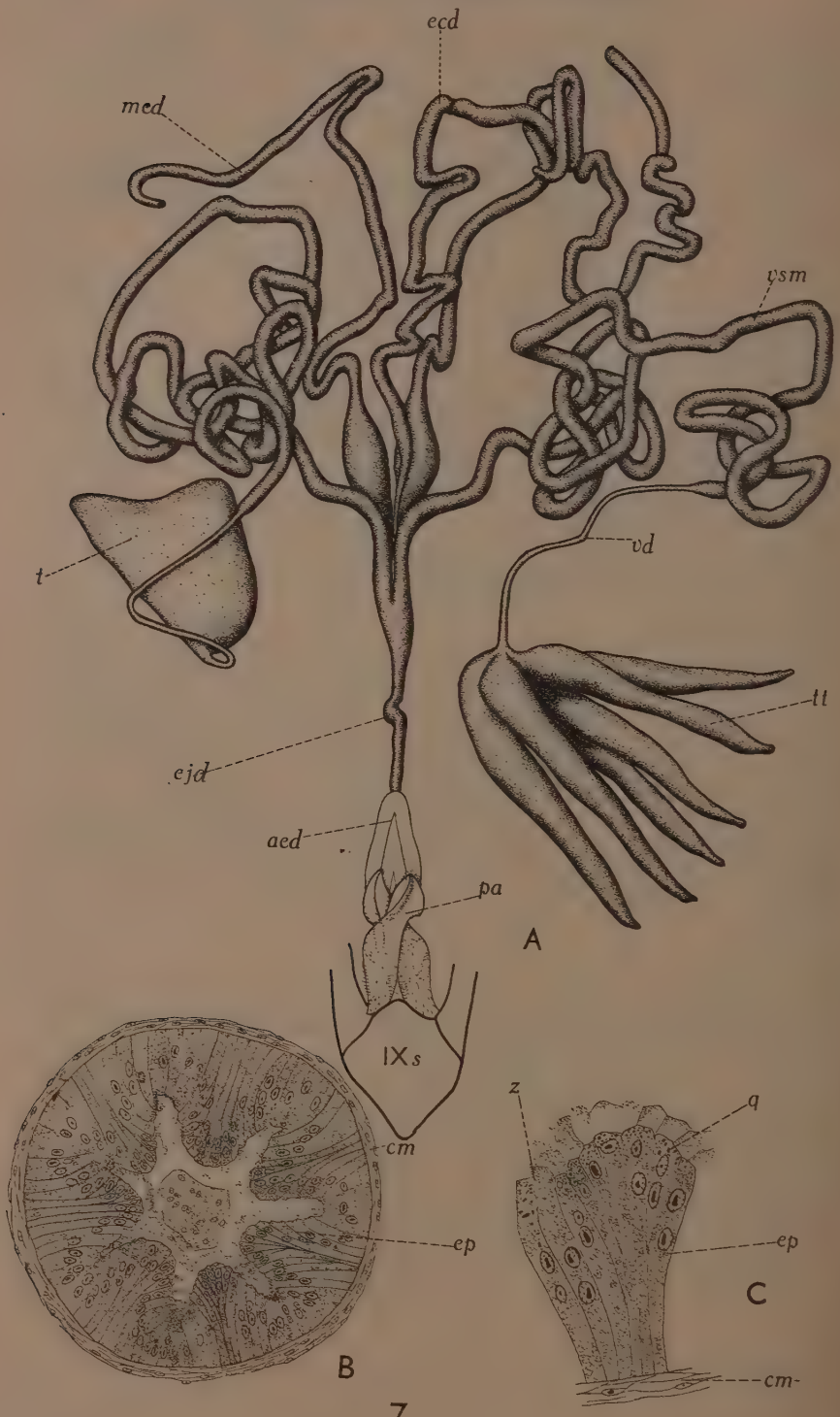
Reproductive System.

Male (fig. 7).

The testes (*t*) lie, one on either side, in the 3rd and 4th abdominal segments. They are held in place by the tracheal branches which ramify over them. Each

Fig. 6.—Transverse sections through the abdomen. A, behind the ninth segment in fourth instar nymph, male. B, posterior region of ninth segment in fifth instar nymph, male, showing the division of the penis lobe by a cleft at x. C, behind the ninth segment in a fifth instar nymph, male, showing the two sub-divisions of the penis lobe. D, posterior region of the seventh segment in a fifth instar nymph, female, showing the spermathecal invagination meeting the common oviducal invagination.

ej., ejaculatory duct; *gc.*, genital chamber; *ism.*, intersegmental membrane; *c. od. inv.*, common oviducal invagination; *pl.*, penis lobe; *pl'.*, lobe which forms the paramere; *pl''.*, lobe which forms the aedeagus; *sp.*, spermathecal invagination.



7

of them consists of seven follicles, which lie enclosed in a peritoneal membrane. The vas deferens (*vd*), which is a fine tube, runs obliquely backwards towards the mid line, dilating into a wider tube—the vesicula seminalis (*vsm*). The coils of the vesicula seminalis of the two sides lie in a bunch in the middle below the intestine. Posteriorly the two tubes run side by side to open into the median ejaculatory duct. The ejaculatory duct is a thick tube which runs posteriorly into the phallus, to open on the outside by the genital pore. In another Heteropteron, *Nezara viridula* L., Malouf described the ejaculatory duct as being made up of two parts—mesodermal and ectodermal—the former muscular and the latter non-muscular. In *Naucoris* there is no such distinction, either developmental or anatomical. As will be seen elsewhere, the ejaculatory duct is entirely ectodermal.

There are two kinds of accessory glands in association with the male generative organs—a pair of mesadenia (*med*) and an ectadenium (*ecd.*). Such glands have not been described to my knowledge for any Hemiptera.

The mesadenia consist of a pair of semi-transparent tubes which lie with their blind ends directed posteriorly on either side of the ejaculatory duct. Each of them runs anteriorly and then turns back to run below the vesicula seminalis of its side, where it dilates out into a club-shaped form. These two swollen structures lie adjacent to each other. Posteriorly they narrow down to open ultimately on either side into the ejaculatory duct at about the same level as the opening of the vesicula seminalis into the latter. The ectadenium consists of a single semi-transparent tube which lies in coils and continues posteriorly as a fine tube between the two vesiculae seminales tubes above and the mesadenia below. It continues into the ductus ejaculatorius.

A transverse section of a testis tubule of a young form shows it to be full of sperm cysts containing spermatogonia. In the adult these are full of spermatozoa.

The vas deferens (*vd*), as also the vesicula seminalis, is lined by a single layer of epithelial cells with indistinct cell boundaries. It is surrounded on the outside by a layer of circular muscle fibres and basement membrane. The lumen of the vesicula seminalis is full of spermatozoa, the heads of which are buried in the epithelium.

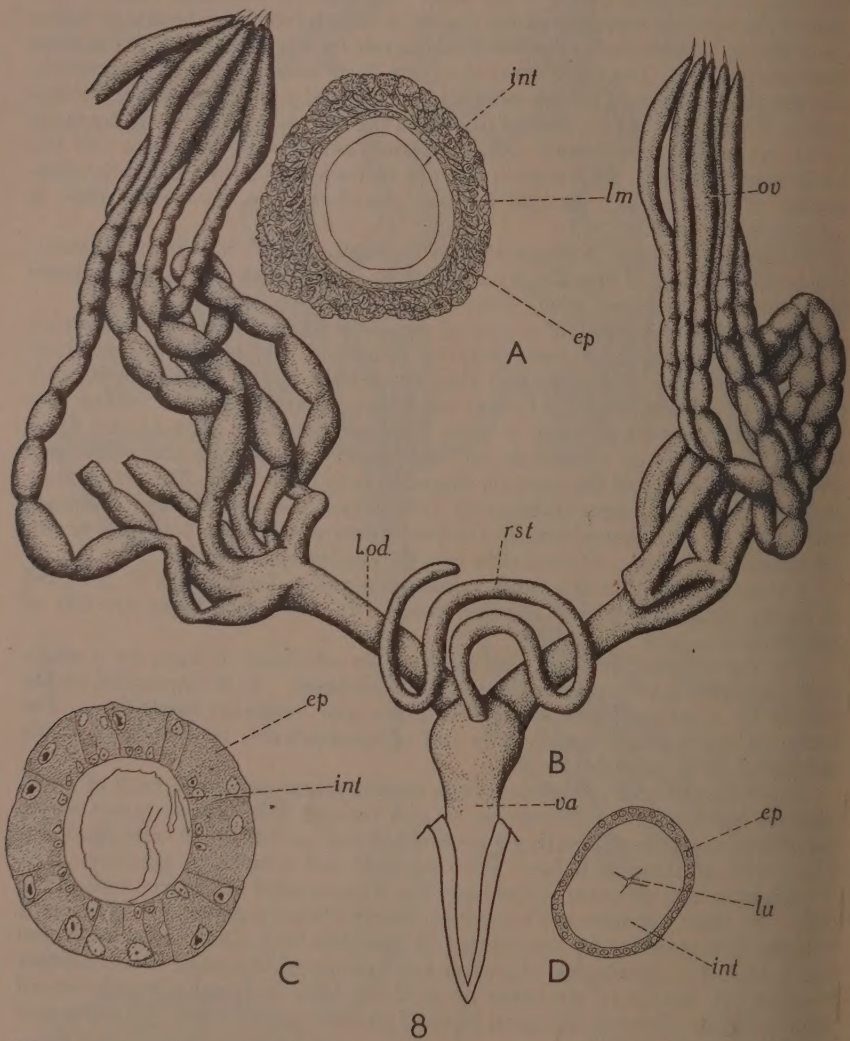
The epithelial cells of the mesadenia consist of secretory cells, each of which contains two nuclei. A transverse section through the swollen region shows the cells arranged in alternating groups of tall and narrow broad cells (fig. 7, B). The nuclei of these cells have large nucleoli and chromatin granules. The cytoplasm is homogeneous at the base, but is vacuolated at the free ends of the cells. In these vacuoles are contained deeply staining granules. These cells liberate their secretion by the rupture of their free ends which lie in the lumen (fig. 7, C). The histological character and manner of liberating their secretion is essentially similar in the other parts of the tube, although the cells are all equally large. There is the usual layer of circular muscle fibres and peritoneal membrane on the outside.

The ectadenium consists of epithelial cells, in which the cell boundaries are

FIG. 7.—A, dorsal view of the male reproductive organs of an adult with the tubes disentangled. B, transverse section of the male accessory gland (mesadenium) passing through the distal region. C, cells of the same.

aed., aedeagus; *cm.*, circular muscle; *ecd.*, ectadenium; *ej.*, ejaculatory duct; *ep.*, epithelium; *med.*, mesadenium; *pa.*, paramere; *q.*, granules in the vacuole at the free end of the cell; *t.*, testis; *tt.*, testis tubule; *vd.*, vas deferens; *vsm.*, vesicula seminalis; *z.*, ruptured end of the cell, liberating secretion.

not clear. These cells are surrounded by a layer of circular muscle fibres and peritoneal membrane.



8

FIG. 8.—A, transverse section of the middle region of the receptaculum seminis. B, dorsal view of the female reproductive organs of an adult with the tubes disentangled. C, transverse section through the distal region, and D, the proximal region of the receptaculum seminis.
ep., epithelium; *int.*, chitinous intima; *lm.*, longitudinal muscle; *l. od.*, lateral oviduct; *lu.*, lumen; *ov.*, ovary; *va.*, vagina.

The ductus ejaculatorius has a simple epithelium lined by a chitinous layer. The layer of circular muscle fibres is extraordinarily well developed and is covered on the outside by the peritoneal membrane.

Female (fig. 8).

There are, in each of the two ovaries, seven ovarioles which extend from the anterior end of the metatergum to the fifth abdominal segment. In Schröder's *Handbuch* it is stated that there are only five ovarioles. The common terminal filament of each side runs anteriorly, where it is attached to the first phragma. During the autumn months the ovary occupies a small space, but during the breeding months of spring and summer it is full of mature ova and occupies a greater part of the abdominal haemocoele. There are 2–3 mature ova in each ovariole, besides 1–2 mature ones present in each of the lateral oviducts.

The lateral oviducts unite with each other in the sixth segment to form the muscular common oviduct (fig. 8, B). It continues posteriorly into the vagina (*vag*), to open on the outside by the female genital aperture.

The receptaculum seminis (*rs*) opens into the vagina dorsally. It consists of a proximal bulbous part and a distal tubular part. During the breeding period the distal tubular part is full of spermatozoa received from the male during copulation.

The ovariole is of the acrotrophic type. It has the same histological structure as described for other Heteroptera.

The lateral oviduct is lined by a layer of convoluted epithelium consisting of secretory cells. These cells contain large nuclei and granular cytoplasm vacuolated at the free ends of the cells. They liberate their secretion in the same manner as the male accessory gland cells. These cells are surrounded by a layer of weakly developed circular muscles and strongly developed longitudinal muscles which are covered by a peritoneal layer. The common oviduct has a similar structure, but in addition has a chitinous intima. The wall of the vagina is convoluted, so that in a transverse section the lumen appears as a vertical narrow space with contorted walls lined with the chitinous intima.

The bulbous part of the receptaculum seminis is a wide sac-like structure which lies dorsal to the vagina. Its wall consists of a single layer of epithelium covered by a thick muscular layer. The distal tubular part is distinguishable into three parts—proximal, middle and distal. The distal part (fig. 8, C) consists of large epithelial cells. There is a layer of small cells towards the lumen, which is lined with a thick chitinous layer. The middle part (fig. 8, A) has a layer of well-developed longitudinal muscle fibres. The proximal part (fig. 8, D) consists of a thin layer of epithelial cells and is lined by a very thick layer of chitin so that the lumen is reduced to a small cavity; this appears cross-like in transverse section. After copulation the spermatozoa were found in the distal and middle parts only.

Summary.

Naucoris cimicoides begins breeding in April, although copulation commences in February. The eggs are inserted in the stems of aquatic plants.

There are five nymphal instars and the total period of development is about 45 days. The process of ecdysis is described.

The male and female reproductive organs are described. In the male there is an ectadenium and a pair of mesadenia. The ovary is of acrotrophic type.

Except for the development of the wings, the air sacs, the parenchymatous cheal organ and the efferent genital ducts and the genitalia, the nymphs resemble the adult.

The entire efferent genital ducts in both sexes, except for the vagina and the ejaculatory duct, are mesodermal. The last two are unpaired and ectoderm in origin. There is no accessory gland in the female, and in the male there is a pair of mesadenia and an ectadenium.

The first and second valvifers are the gonocoxites of the eighth and ninth abdominal segments respectively. The first and second valvulae represent the gonapophyses of the eighth and ninth segments respectively. The third valvulae are the drawn-out processes of the second valvifers.

The aedeagus and parameres arise from a pair of buds—one on either side of the mid line—appearing in the intersegmental region between the ninth and tenth abdominal segments. They probably represent the appendages of the tenth abdominal segment.

Literature.

Brocher, F., 1913, *L'aquarium de chambre*. Paris.

Butler, E. A., 1923, *A Biology of the British Hemiptera–Heteroptera*. London.

Christophers, S. R., and Cragg, F. W., 1922, On the so-called " Penis " of the Bed-bug (*Cimex lectularius* L.) and on the homologies of the male and female genitalia of this insect. *Ind. J. med. Res.* **9** : 445–463.

Denny, A., 1897, On the development of the ovipositor in *Periplaneta orientalis*. *Commemoration Volume* : 169. Sheffield.

Dufour, L., 1833, Recherches anatomiques et physiologiques sur les Hemipteres. *Mem. Sav. Acad. Sci. Paris* **4** : 131–461.

Else, F. L., 1934, The developmental anatomy of male genitalia in *Melanoplus differentialis*. *J. Morphol.* **55** : 577–610.

George, C. J., 1928–29, The morphology and development of the genital ducts of Homoptera and Zygoptera as shown in the life-histories of *Philaenus* and *Agrion*. *Quart. J. micr. Sci.* **62** : 447–495.

Heymons, R., 1899, Beiträge zur Morphologie und Entwicklungsgeschichte der Rhynchoten. *N. Act. k. Leop. Carol. Akad. Naturf.* **74**.

Malouf, N. S. R., 1933, Studies on the internal anatomy of the " Stink Bug," *Nezara viridula* L. *Bull. Soc. R. ent. Egypte* **1933** : 96–119.

Mehta, D. R., 1933, On the development of the male genitalia and the efferent genital ducts in Lepidoptera. *Quart. J. micr. Sci.* **76** : 35–61.

Metcalfe, M. E., 1932, The structure and development of the reproductive system in Coleoptera with notes on its homologies. *Ibid.* **75** : 47–129.

——, 1932, Notes on the Structure and Development of the Reproductive Organs in *Philaenus spumarius* L. *Ibid.* **75** : 467–481.

——, 1933, Notes on the Structure and Development of the Female Genital System in *Dasyneura leguminicola*. *Ibid.* **76** : 89–106.

Pruthi, H. S., 1924, The development of the male genitalia of Homoptera with preliminary remarks on the nature of these organs in other insects. *Ibid.* **69** : 59–96.

——, 1924, On the post-embryonic development and homologies of the male Genital Organs of *Tenebrio molitor* L. *Proc. zool. Soc. Lond.* **1924** : 857–868.

——, 1925, The morphology of the male genitalia in Rhynchota. *Trans. ent. Soc. Lond.* **1925** : 127–267.

Roonwal, M. L., 1937, Studies on the embryology of the African Migratory Locust, *Locusta migratoria migratorioides*. *Phil. Trans. Roy. Soc.* **227** : 175–244.

Rousseau, R., 1921, *Les Larves et Nymphes Aquatiques des Insectes d'Europe* **1**. Bruxelles.

Snodgrass, R. E., 1931, Morphology of the insect abdomen, I. *Smithson. misc. Coll.* **85** (6).

——, 1933, Morphology of the insect abdomen, II. *Ibid.* **89** (8).

——, 1935, *Principles of insect morphology*.

——, 1936, Morphology of the insect abdomen, III. *Smithson. misc. Coll.* **95** (14).

——, 1937, The male genitalia of Orthopteroid insects. *Ibid.* **96** (5).

Zander, E., 1903, *Der Stilplan des mannlichen Genital Apparates der Hexapoda*. Erlangen.